teeth and the head two frontal tubercles, which, however, are much smaller than in any other species of the group, and followed behind by a broad but shallow frontal cavity. The clypeus is pointed and recurved; the mandibles without trace of tooth on their outer edge. The thorax is as broad as the elytra, broadly rounded on the sides, slightly narrowed to the base, with acute hind angles; the surface free from furrows and strongly and sparsely punctured, the punctures on the disk larger and transverse-oval or oblong; on each side of the anterior disk is a small round fovea. The rows of small circular punctures on the elytra are obliterated on the sides posteriorly and on approaching the apical callus. The hind tibiæ have no trace of spine on their outer edge (only a few short setæ), but there is a long spine at their outer apex. The species therefore is intermediate between Burmeister's subgroups *a* and *b*. The basal joint of the hind tarsi is not prolonged into a spine. The pygidium is opaque and punctured; the apical ventral segment very finely punctured, the rest of the abdomen (except the extreme sides) being smooth. The metasternum is punctured on the sides and clothed with reddish hair.

4. On a hitherto unrecognized Feature in the Larynx of the Anurous Amphibia. By G. B. Howes, F.Z.S., F.L.S., Assist. Prof. of Zoology, Normal School of Science and R. School of Mines, S. Kensington.

[Received June 2, 1887.]

The general structure of the respiratory organs in the Amphibia was first carefully analyzed by Henle, nearly fifty years ago[1]. He showed that well-developed laryngeal cartilages are nearly always present, and that the trachea and bronchi, though subject to considerable variation, may be supported by cartilaginous elements also. Conspicuous among recent investigators in the same field is Wiedersheim. He has shown[2] that in the Gymnophiona, as in some Urodeles (e. g. *Siren* and *Amphiuma*), trachea and bronchi are well differentiated, and that fully formed cartilaginous rings may be developed in connection therewith. To him we are also indebted for a description of the larynx of *Rana esculenta* in all its details[3], and for a number of other observations upon the subject generally; while he has summed up our knowledge of this in his Text-book of Vertebrate Anatomy. Dubois is now engaged upon a searching investigation into the morphology of the larynx. He calls attention in his preliminary notes[4] to the presence, among other things, of

[1] 'Vergleichende anatomische Beschreibung des Kehlkopfs:' Leipzig, 1839.

[2] 'Die Anatomie der Gymnophionen:' Jena, 1879. *Cf.* also his 'Lehrbuch d. vergleich. Anatomie d. Wirbelthiere.'

[3] Originally in his 'Lehrbuch,' edit. i. vol. ii. 1882, pp. 640–645.

[4] "Zur Morphologie des Larynx," Anat. Anzeiger, vol. i. 1886. See also Van Bemmelen, Zoolog. Anzeiger, vol. x. 1887, p. 91.

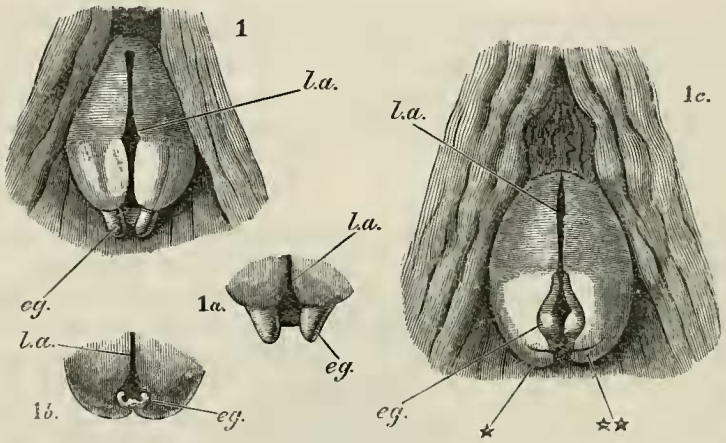
median procricoid (interarytenoid) elements in the Amphibia—an interesting feature of comparison with the higher types.

The Amphibian larynx is, like that of Reptiles, chiefly remarkable for the absence of a distinct thyroid cartilage; but the above *résumé* shows that with this exception there are represented in the respiratory organs of the Amphibia, as a group, the leading constituents of those of the higher Amniota. The epiglottis would, however, appear to be absent; and it is the object of this paper to inquire how far this is really the case.

It is necessary to point out that Henle wrote[1] of '*Engystoma*' that "die Constrictoren des Stimmladeneingangs sind bei diesen Species nur sehr lose an die Stimmlade befestigt, sie liegen in einer Querfalte der Schleimhant hinter der Zunge und dem Eingang der Stimmlade, und diese Falte bedeckt, wie eine Epiglottis, der vordersten Theil des Eingangs der Stimmlade."

My attention was first drawn to this subject two years ago, while dissecting a male of the Grass-Frog (*R. temporaria*). In that specimen (fig. 1 *a*)[2] the front wall of the larynx was prolonged forwards

Fig. 1.



The larynx in *Rana*. 1. *R. esculenta*, young ♂. 1 *a*. *R. temporaria*, ♂. 1 *b*. *R. temporaria*, ♂. 1 *c*. *R. temporaria*, ♀. All magnified three times.
eg, epiglottis; *l.a*, aditus laryngis.

into two papillate folds (*eg.*), which were tumid and connected together by a thin film, the whole constituting a forward prolongation of the laryngeal mucous membrane apparently superadded to that which is customary. Wiedersheim, in describing the larynx of *R. esculenta*, points out[3] that it lies immediately behind a deep depression of the mucous membrane which corresponds with the

[1] *L. c.* p. 28.
Originally figured in 'Atlas of Elem. Biology,' pl. i. fig. 13 (1885).
'Die Anatomie des Frosches,' Ecker and Wiedersheim, pt. 3, p. 8 (Brunswick, 1882).

hinder border of the body of the hyoid. This was so in the specimen to which I have just referred, and the anterior prolongation described overhung this depression, in a manner strikingly suggestive of the epiglottis.

Hoil[1] and Royer and Bambecke[2] have most recently studied the anatomy of the mouth in the Anurous Amphibia: the first-named author deals chiefly with histological details in *R. temporaria*; the last-named deal with the subject in general; but I fail to find mention, in their writings, of those facts with which I am concerned. I am satisfied that the structures described above may or may not be present in individual examples of the common Frog, and have found, to my surprise, that the free anterior extremity of the larynx is subject to no inconsiderable amount of variation in it, to say nothing of the Anura as a group.

If the lips of the laryngeal aditus be examined with care in *R. temporaria* there will generally be found at its anterior end folds identical with those here figured, but more or less marked. They are sometimes so small that there is little wonder they should have been so long overlooked. They are well differentiated from the rest of the larynx; of a yellowish colour in life and soft and fleshy, projecting freely beyond those parts which are supported in cartilage (*cf.* figs. 1, 1 *a*, *eg*). There generally passes between them a thin transverse fold of mucous membrane, and occasionally, when very minute, they are, together with the same, erected and closely applied to the front face of the larynx (figs. 1 *b* and 3). I was for some time disposed to think that they might be peculiar to the males; but that this is not the case the larynx of an adult female, represented in fig. 1 *c*, will show. That specimen is further remarkable, among the larynges of a number of females which I have examined, for the fact that the folds were continued along the sides of the aditus, the anterior half of that being thus embraced by a hood-shaped lip.

On examining other members of the group, it early became obvious that the structure with which we here have to deal was by no means exceptional. In *Leptodactylus pentadactylus* and the Bull-Frog (*R. pipiens*), for example (figs. 2 and 3), two papillate elevations were found to be present; these were in both cases small and erected, and united by a transverse fold as in the first-named example. Comparison of figs. 1 *b* and 2 reveals an absolute identity between individuals of *R. temporaria* and *Leptodactylus pentadactylus*.

In two of the above-named species I found, in addition to the foregoing, a couple of other folds which were related to the hind half of the aditus (*ep*, figs. 2 and 3). In the Bull-Frog (fig. 3) they passed insensibly into the mucous membrane posterior to the larynx; but in *Leptodactylus* (fig. 2) they united behind so as to form an insignificant lip which embraced the hind boundary of the aditus, much as did the supposed epiglottis its front one. I have not seen

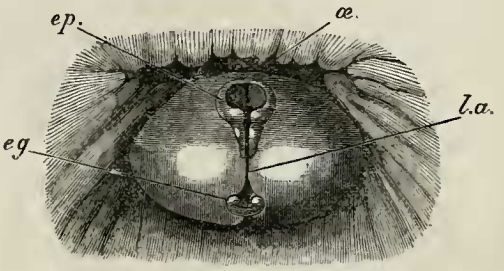
[1] Sitzungsb. Wien. Akad., Jan. 1887.

[2] "Sur les caract. fournis par la bouche des têtards des Batraciens anoures d'Europe," Bullet. Soc. Zool. d. France, 1881, p. 75.

these folds in either the Grass or Edible Frogs. I propose to term them, in accordance with their position, *epilaryngeal folds*.

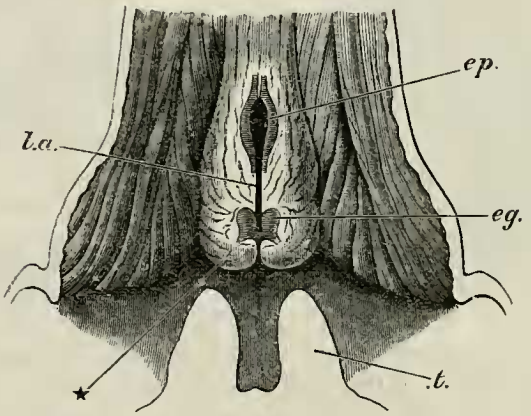
At this stage two difficulties presented themselves. Firstly, as to the epilaryngeal folds. Their condition, as seen in the Bull-Frog, might conceivably be such as would have resulted from puckering of a loose membrane under muscular contraction; while their sym-

Fig. 2.



The larynx in *Leptodactylus pentadactylus*, ♂, front view. Magnified two and a half times.

Fig. 3.



The larynx in *Rana pipiens*, ♀, top view. Magnified twice.
eg, epiglottis; *ep*, epilaryngeal folds; *l.a*, aditus laryngis; *t*, tongue; *œ*, œsophagus.

metry and union in *Leptodactylus* pointed, no less distinctly, to the conclusion that they were definite and permanent structures. Doubt was dispelled on examination of other genera, for in a male of *Ceratophrys americana* (fig. 4) the two folds not only united behind but gave rise to a clearly differentiated overhanging lip, *ep.*, such as could only have been a permanent structure.

Secondly, as to the anterior folds, *eg*. As already stated, I at first took these to represent the epiglottis of the higher Amniota; but

their paired nature, which is most conspicuous throughout, remained for some time a stumbling-block in the way of that interpretation. His, however, has shown that the human epiglottis and plicæ ary-epiglotticæ are formed from a primarily paired structure. He describes them[1] as arising within what he terms the 'mesobranchial area,' from the modification of a couple of conjoined papillate folds or 'furcula.' In other words, the human epiglottis is, according to him, a strictly bilaterally symmetrical structure. Comparison of his description and figures (see especially fig. 44, p. 66, *l. c.*) with those here given shows that there is no important difference, either in position or origin, between the developing human epiglottis and the epiglottidean folds of the Anura; but it also introduces a fresh difficulty, on account of the presence in the latter of a couple of tumid

Fig. 4. Fig. 5.

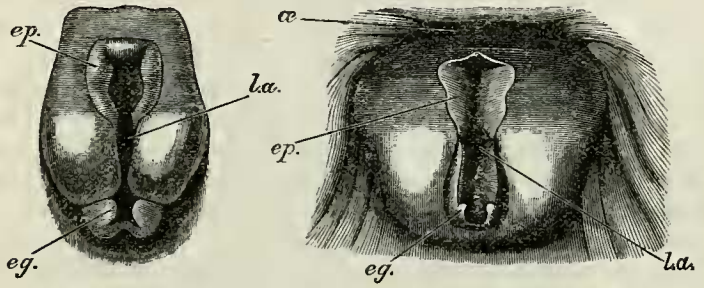


Fig. 4. The larynx in *Ceratophrys americana*, ♂. Magnified three times.
Fig. 5. The same in *Calyptocephalus gayi*, ♂. Magnified twice.
References as in figs. 2 and 3.

folds below those which I have thus far described (* figs. 1 *c* and 3). These might conceivably represent the furcula of His. They are, however, exceedingly inconstant, and in numerous instances unrecognizable; fig. 3 represents their maximum development observed. In one instance I noted (*R. temporaria*, ♀, fig. 1 *c*) that they were asymmetrical, that of the left side being much the smaller of the two[2]; and this at once suggested that they might be accidental and due to displacement. From careful study of both living and preserved specimens, I am fully satisfied that this is the case. Careful dissection has shown me that they are mere displacements of the mucous membrane, varying with the degree of contraction of the constrictor laryngis and petrohyoid muscles, and I regard them, moreover, as identical with that fold described by Henle in *Engystoma*, and likened by him to the epiglottis, as already stated.

The facts before us go far to justify the view that the epiglottidean folds of the Anura are homologous with the epiglottis of Mammals in its most typical form; a striking difference, however, suggests itself when comparing the two more closely. The Mammalian epiglottis is always chondrified, and in direct relationship with the

[1] 'Anatomie menschlicher Embryonen,' pt. 3, p. 60 *et seq.* Leipzig, 1885.
[2] Insufficiently expressed in the woodcut, at **.

thyroid cartilage; in the Amphibia, on the other hand, the epiglottidean fold is entirely membranous and in direct connection with the arytenoids, the front faces of which it surmounts (fig. 9, *eg.*). This difficulty, however, vanishes when it is considered that all recent investigation goes to show that the epiglottis is a secondary structure, formed independently of the rest of the larynx, and subject to the greatest variation. Dubois states[1] that in Mammals it represents a chondrification of the submucous tissue of the glosso-laryngeal fold, and that it only secondarily comes into connection with the thyroid cartilage. Clearly, then, the absence of a thyroid cartilage in the Amphibia cannot militate against my view. The same author further states that the epiglottis is present only in Mammals; but comparison of figs. 1, 1 *a*, 4, with His's figures of the human embryo referred to, shows that that is certainly not the case. Consideration of the above facts, taken collectively, forces us to the conclusion that the epiglottis may be represented in Anurous Amphibians, and that in a form most nearly realizing, so far as our present knowledge carries us, the initial stage in its development in man himself.

The interest attaching itself to the discovery of the epiglottis in Amphibia is self-evident, and it opens up questions of no little morphological importance. Future investigation must decide how far that which is customarily termed the epiglottis in some Reptiles[2] and Birds may or may not correspond with that of Mammals.

A consideration of the functional significance of this organ, as here described, reveals some interesting facts. Examination of the figures shows at once that the Amphibian epiglottis cannot have much, if anything, to do with deglutition. The classical Johannes Müller was one of the first to insist[3] upon the functional importance of the Mammalian epiglottis as a voice-organ; and it is now clearly established[4] that while that structure is not essential to deglutition, either of solids or liquids, it is indispensable to the full exercise of the voice, playing a part in phonation of unexpected importance.

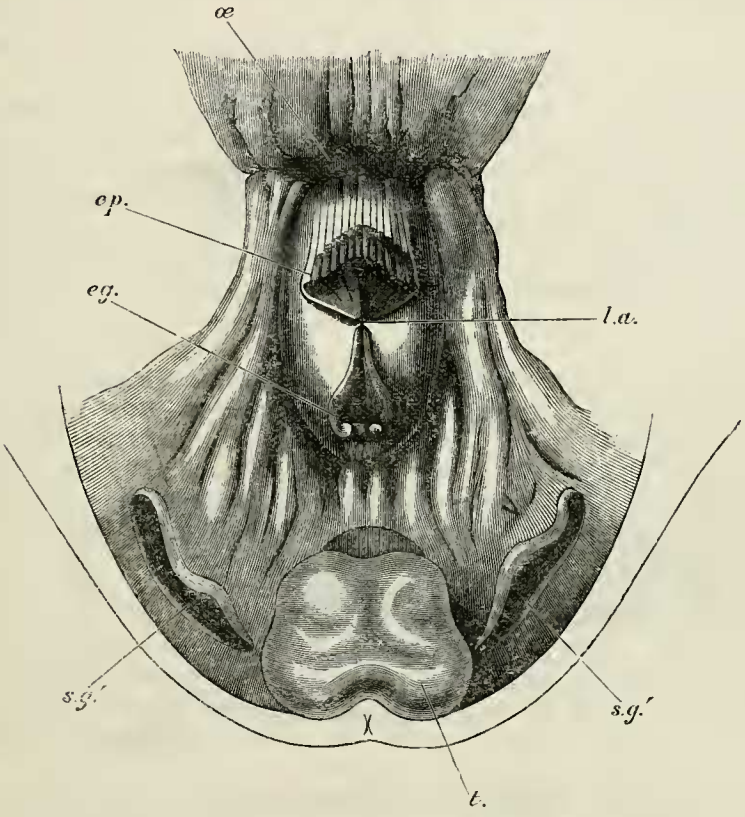
Turning to the Amphibia, it is satisfactory to note that nothing at all comparable to that which I have described is forthcoming among the tailed forms. The epiglottis is clearly appearing among the Anura; and it becomes a question of the highest interest to inquire, in the knowledge of the above physiological facts, whether its relative development is in any way associated with that of other accessories to the voice, so well known in the males of certain genera.

Henle long ago called attention (*l. c.*) to the existence of minor sexual differences in the laryngo-tracheal skeleton in *Pipa* and other Anura. I have already shown that traces of both the epiglottis and epilaryngeal folds may be found in females of certain species (figs. 1 *c* and 3); and, on turning my attention to the proposition above named, I was, at first, awarded with unexpected success. In a male of

[1] *L. c.* p. 186.
[2] *Cf.* Henle, *l. c.* pp. 51, 52, and 60, 61.
[3] Handbuch d. Physiologie, 1840.
[4] Walton, "The Function of the Epiglottis," Journ. of Physiology, vol. i. 1878-9.

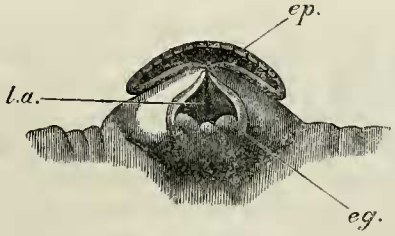
Ceratophrys americana (fig. 4, p. 495) both epiglottis and epilaryngeal folds were found to be well developed; but though conspicuous, they remain comparatively insignificant beside those of an adult male of

Fig. 6.



The larynx and floor of the mouth in *Chiroleptes australis*, adult ♂.

Fig. 7.

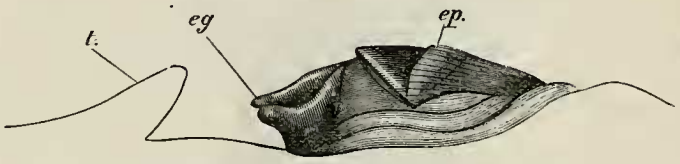


The larynx in the same, seen *en face*. Both figs. magnified twice.
References as in previous figures. *s.g'*, orifice of gular sac.

Chiroleptes australis, that being one of the genera possessed of the well-known gular sac (*s.g*, *s.g'*, figs. 6 and 9). This specimen presents the maximum development observed, and I have accordingly figured

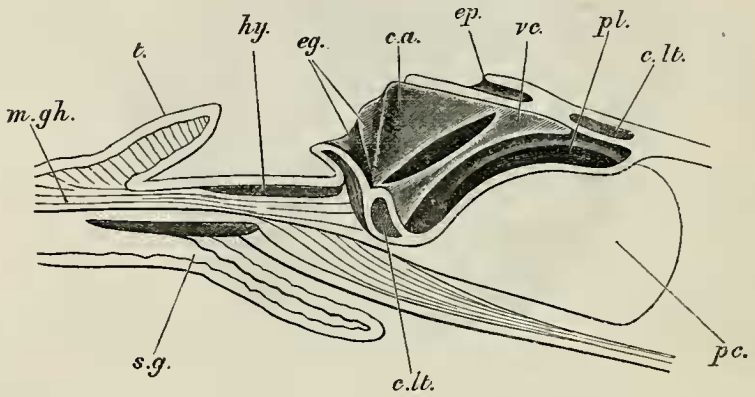
it (figs. 6 to 10) in all its important aspects. The interest of it is vastly increased when it is stated that in a female which I have examined the folds were absent, while in a second male they were insignificant [1]—facts which point to the conclusion that their development takes place comparatively late in life, in all probability correlatively with sexual maturation.

Fig. 8.



The larynx in *Chiroleptes australis*, side view.

Fig. 9.



The same, in longitudinal section.

References as in previous figures. *c.a*, right arytenoid; *c.lt*, cricoid (laryngo-tracheal) cartilage; *hy*, body of hyoid; *m.gh*, genio-hyoglossus muscles; *pc*, pericardium; *pl*, entrance to right lung; *s.g*, gular sac; *vc*, right vocal cord.

Figs. 6 to 9 will show how fully the two structures may be developed. The epiglottis, *eg.*, stands out prominently in front; the epilaryngeal fold is hood-shaped, overhanging the hinder third of the aditus, and the two together embrace the lateral walls of the aditus for nearly its whole extent—so much so, that I at first took them to be continuous. This, however, is not the case, and here, as in all other examples with which I have met, the two structures, although they may approximate, are perfectly distinct (*cf.* fig. 5). The epilaryngeal fold is entirely membranous, exhibiting on its upper part, which is

[1] For the opportunity of examining these two specimens, as for further assistance, I am indebted to the courtesy of Mr. Boulenger, F.Z.S., of the National Museum at South Kensington.

thinner and more vibratile than the rest, a beautiful parallel striation; the epiglottis is also membranous, but supported upon a connective-tissue framework, which is densest along the lines of development of its paired outgrowths. Neither epiglottis nor epilaryngeal folds appear to have given attachment to definite muscles; the epiglottis was very flexible in life; and although unable to trace a direct muscular connection, I incline to the belief that it was under muscular control.

What may be the precise function performed by these interesting structures, I do not pretend to say, but I hold it indubitable that they are concerned in phonation. If this be admitted, a most interesting parallelism becomes obvious between the higher Amniota (Mammalia) and the higher Ichthyopsida (Anura) with respect to the appearance of the epiglottis as an accompaniment of specialized laryngeal activity; and we have good reason for believing that organ to have been primarily connected with phonation—a deduction which all recent investigation into the function of the Mammalian epiglottis upholds.

While the epiglottis makes its appearance in the Amphibia as an accessory voice-organ, its development does not appear to be of necessity related to a high development of the vocal sac. Heron Royer has lately described[1] the larynx of *Hyla meridionalis* (*barytonus*, Royer); in it, in spite of the immense development of the gular sac, there does not appear to be anything present of the nature described above. Royer has further pointed to specific differences between the larynges of *H. arborea* and *H. meridionalis*; Mr. Boulenger, however, informs me that he has found the same to be of no specific value, and I fully share that belief.

Thanks to Prof. Huxley and Mr. Boulenger, I have been able to examine a series of specimens, with the result set forth in the following table[2]:—

a. Epiglottis present: epilaryngeal folds confluent behind.

Calyptocephalus gayi. ♂.	*Heleioporus albopunctatus*. ♂.
Ceratophrys americana. ♂.	*Leptodactylus pentadactylus*. ♂.
Chiroleptes australis. Adult ♂.	

b. Epiglottis present; epilaryngeal folds not confluent behind.

Hyla cærulea. ♂.	*Hyla lichenata*. ♀.
*—— *dolichopsis*. ♂, ♀. (A second ♂ showed no traces.)	**Rana pipiens*. ♂, ♀.

c. Epiglottis present, but small; epilaryngeal folds absent.

**Bombinator bombinus*. ♂.	**Rana esculenta*. ♂, ♀.
Chiroleptes alboguttatus. ♂.	*—— *temporaria*. ♂, ♀.
—— *australis*. ♂ juv.	

[1] "Note sur une forme de Rainette nouvelle pour la faune française," Bullet. Soc. Zool. d. France, vol. ix. 1884.

[2] One specimen only examined, excepting those marked *.

d. Epiglottis and epilaryngeal folds both absent.

Bufo typhonius. ♀.
Cornufer vitianus. ♀.
**Hyla meridionalis.* ♂, ♀.
—— *venulosa.* ♂.
**Hylodes martinicensis.* ♀ juv.
Nannophrys ceylonensis. ♂.
Phryniscus lævis. ♀.
Phyltomedusa bicolor. ♂ juv.
**Rana esculenta.* ♂, ♀.
*—— *temporaria.* ♂, ♀.
—— *temporalis.* ♂.
Rappia marmorata. ♀.
Rhacophorus maculatus. ♂, ♀.
Rhinoderma darwini. ♂.
Xenophrys monticola. ♀.

Perusal of the above brings into prominence a wide range of individual and specific variations. The former are, however, less striking than appears at first sight, and little more remarkable than those of the Amphibian manus and pes, or of the Batoid intestinal valve[1]; the latter find a near parallel in the modifications of the larynx in certain fruit-eating Bats recorded by Dobson[2]. That observer has obtained a satisfactory explanation of the phenomena upon purely physiological grounds, and the analogy suggests that an investigation into the habits of the living Anura under consideration might furnish a similar clue. If, as the analogy to *Chiroleptes* would suggest, the folds in question are associated with the development of vocal sacs, it is difficult to reconcile their absence in *Hyla meridionalis* and *H. venulosa*, with their presence in *H. dolichopsis* and *Bombinator*; while the combination met with in *Heleioporus* would appear to negative the supposition. It may be held that the structures are developed periodically or with sexual maturation; but, if so, it becomes hard to account for their insignificance in the male of *Leptodactylus* (fig. 2), in which the accessory spurs had attained a considerable development. The facts adduced in *Chiroleptes australis*, while they appear to favour this belief, are, in themselves, capable of a different interpretation, for that the differences between the two males which I have examined are due to age is a surmise. The facts are very puzzling; but who is to say that, in the most marked cases recorded, we may not be dealing with a character of taxonomic value, fit at least to rank with those customarily relied upon[3].

Apart from the above considerations, examination of the figures shows most conclusively that, in the specimens which I have described, a gradational modification can be traced. *Chiroleptes* (fig. 6) and *Rana* (fig. 1 *b*) stand at opposite ends of a series, the intermediate steps in which are furnished by *Ceratophrys*, *Leptodactylus*, and *Rana pipiens*, in succession. The question therefore arises as to which of the two first-named typifies the more primitive arrangement.

[1] T. J. Parker, T. Z. S. 1880, pp. 49–61.
[2] P. Z. S. 1881, pp. 685–93.
[3] *Cf.* remarks by Huxley on the "Taxonomy of the Canidæ" (P. Z. S. 1880, p. 286), and by Herdman, "On the Specific and Local Variations in the Tunicata (First Report of the Liverpool Marine Biological Committee, 1886, pp. 355, 356).

If the apparatus be held to be of none but physiological significance, the clue to its meaning has yet to be found; it is clearly in no way associated with the development of the vocal sac, nor is it confined to the males, as might be supposed. In the higher forms, however, it is vestigial and of little or no functional importance; and there is nothing forthcoming in any one specimen which is not represented in the male of *Chiroleptes*. These facts, in view of the uniformity of development of the parts in the latter, would seem to me to suggest that the apparatus has an important morphological significance, and that in the admittedly lowly Australian type the primitive condition is most nearly exemplified. The problem is an interesting one, and further investigation is necessary for its solution.

Turning, finally, to the question of general morphological importance, it is clear that the discovery of the epiglottis in the Amphibia, in the form and under the conditions here recorded, carries back a stage further the initiation of one more structure peculiarly characteristic of Mammals. The interest of this is increased when we reflect upon the identity of the Amphibian epiglottis, which is clearly bilaterally symmetrical, if not actually paired, with the initial phase in development of that organ in the human subject as observed by His. The facts show that the origin of this typically Mammalian structure must be sought in animals lower than the living Lizards[1]. It would be wide of the mark to form data for discussing the question of Mammalian affinities upon it. In view, however, of the anticipation of the cæcum coli in the Common Frog[2], and of the excursions made by those Amphibia with suppressed larval metamorphoses[3], in which it is highly probable there may have been foreshadowed the fœtal membranes of the Amniota (*cf.* Huxley, P. Z. S. 1880, p. 660), the facts here recorded can best be regarded as indicative of similar excursions towards the elaboration of the voice-organ, anticipatory, as has been shown, of the characteristically Mammalian condition.

[1] It is of interest here to note the existence of an epiglottis-like fibro-cartilaginous plate in *Protopterus*. Attention was first drawn to it by Henle (*l. c.* pp. 5, 6), and it was shortly afterwards described in full and figured by Bischoff ("Descr. Anat. du *Lepidosiren paradoxa*," Ann. Sci. Nat. t. xiv. Zool. 1840 p. 136). Wiedersheim has refigured it ('Lehrbuch') and recorded (*ibid.*) the discovery of an analogous structure in *Lepidosteus*.

[2] Huxley, in Huxley and Martin's Elem. Biology, 1875, p. 166.

[3] Especially *Nototrema*, Weinland, Archiv f. Anat. und Phys. 1854; *Hylodes*, Peters and Gundlach, Monatsb. Berlin. Acad. 1876; *Rana opisthodon*, Boulenger, T. Z. S. vol. xii. 1886; *Phyllomedusa*, v. Ihering and Boulenger, Ann. & Mag. Nat. Hist. vol. xvii. 1886.

For a *résumé* of the subject generally, with full references and list of species, see Boulenger on *Phyllomedusa*, *op. cit.* p. 464. *Cf.* also Smith and Cope on *Dendrobates*, Amer. Naturalist, 1887, pp. 307–311.